Vol. 75, Part 2, pp. 218-230. Plates 14–16. 1 Fig.

The Life Cycle of the Heterophyoid Trematode *Telogaster opisthorchis* n.g., n.sp.

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There is little recorded knowledge of trematodes from New Zealand hosts. In the Index compiled by Hutton (1904) thirty species of digenea are mentioned. The explanation of this record was given by Dr. W. B. Benham: "Rudolphi and others described the flukes from hosts which occur in European waters, but the hosts occur also in and around New Zealand. It is therefore likely that they will harbour the same species of parasites, hence Hutton included them in his Index—perhaps prematurely."

Trematodes first received notice in New Zealand in the reports of the Livestock Division of the Department of Agriculture from 1897 onward. The occurrence and spread of *Paramphistomum cervi* and *Fasciola hepatica* was recorded, but nothing was known of the local hosts.

Observations were made by Monticelli (1899) on specimens of *Gyrocotyle rugosa* Diesing and *Distomum veliporum* Creplin which had been sent to the British Museum from Dunedin. In 1904 Chilton noted that a pectinate cercaria parisitised the gills of *Chione stutchburyi* at Portobello. Twenty-three years later Hopkirk (1927) found that the snails *Potamopyrgus antipodum* and *P. corolla* carried four cercariae in the North Island. From his descriptionns these parthenita appear to include *Coitocaecum anaspidis, Telogaster* n.g. and *Opechona* sp.

An account of the hosts and bionomics of *Fasciola hepatica* in this country was published by Macfarlane (1937). The life cycle of *Coitocaecum anaspidis* (Macfarlane, 1939) and the occurrence of schistosome dermatitis in the southern lakes (Macfarlane, 1944) have been investigated.

The present paper deals with the morphology, development, life cycle and taxonomy of a new genus, the adult of which is an intestinal parasite of freshwater eels. The main habitat studied was the Heathcote River, Christchurch; but the Selwyn River and a tributary of the Cass were also extensively examined.

Morphology.

The Adult.

Superfamily: HETEROPHYOIDEA, Faust, 1929.

Family Cryptogonimidae, Ciurea, 1933.

Genus Telogaster nov.

Telogaster opisthorchis nov. gen., n.sp.

The adults of this trematode parasitise the posterior two-thirds of the intestine of the eels *Anguilla dieffenbachii* and *A. australis schmidtii.*

The body has the shape of a long ellipse. The acetabulum is one-third the diameter of the oral sucker, and its centre is not quite

one-third of the length of the body from the anterior end. Probably the chief function of the acetabulum is to assist in copulation. Most of the extensions of the animal take place in the preacetabular region.

Dimensions of *Telogaster* when sexually mature have the following range: Length 1·1–1·95 mm., width 0 28–0·56 mm., oral sucker 0·19–0·23 mm., acetabulum 0·11–0·13 mm., acetabulum from the anterior end 0·38–0·50 mm., prepharynx 0·06–0·08 mm., oesophagus 0·46–0·63 mm., caecum 0·28–0·37 mm., right testis 0·23 x 0·15–0·27 x 0·17 mm., left testis 0·26 x 0·16–0·38 x 0·23 mm., ovary 0·12 x 0·19–0·19 x 0·22 mm., cephalic spines 0·047–0·052 mm., eggs 0·030 x 0·017–0·033 x 0·019 mm.

Spines, showing a progressive decrease in size posteriorly, completely cover the cuticle. Each spine (·008 mm. long in the head region) is directed backwards, but is largely buried in the cuticle. The spines lie in transverse rows, alternating in successive rows. Around the mouth are the cephalic spines 0·05 x 0·01 mm. when fully grown. The number of spines ranged from 22 to 34 in 85 specimens. The mean count, 26·9, does not coincide with the mode, 25. Most of the animals, however, fall into the groups with 25 to 28 spines. The curve is slightly skewed, but the normal formula for standard deviation may be applied: S.D. of mean $= 26{\cdot}9 \pm 2{\cdot}4$. This variation is not due to functional loss, since metacercariae show an equal range; nor is it due to local races. There is also a teratological variation in number of spines, chiefly among full-grown metacercariae. In these animals spines 0·05 mm. long are either completely or incompletely divided into two. (Plate 14, fig. 6.) When completely divided, one member of a pair may be shorter than the other, and both may be flattened on their approximated sides. Some spines fail to develop to more than 0·02 mm. long, while in other cases there is an increase in number of deformed spines up to 48.

Unicellular gland-like bodies open through the cuticle of the anterior half of the adult, and are present down to the posterior end of the acetabulum.

The *alimentary system* is dorsally placed and has the following parts: Mobile sphincteric lips surround the terminal mouth. The oral sucker is small and ovoid when contracted, changing to a truncated cone when relaxed. The prepharynx has a sphincteric opening onto the oral sucker, and is provided with longitudinal and circular muscles. At rest the pharynx closes in its posterior half while the anterior half remains open. From the pharynx the oesophagus continues backwards to a point midway between the acetabulum and the ovary, where it bifurcates to form the caeca. The oesophagus shows no definite epithelial cells, but it has a powerful musculature. The caeca are about half the length of the oesophagus and twice its diameter. Immediately after the division of the oesophagus the digestive epithelium begins, an observation made remarkably clear when $\frac{1}{1,200,000}$ neutral red is used on living material (Koehring, 1930). No staining takes place in the oesophagus, but the cells and the contents of the lumen of the caeca are coloured a brownish red in 1½ hours. Later much of the stain leaves the cells, but the chyme becomes bright red. The living columnar

epithelial cells are, from the outside, polygonal bodies 0·02 mm. long with large nuclei. (Plate 15, fig. 10.) In sections the epithelium is seen to rest on a basement membrane, outside which lie muscle fibres. The nuclei lie at the proximal end of the cells, whilst medially and distally there are large, clear vacuoles of secretion. Distally there is a non-staining region. That enzymes are produced is indicated by the neutral red reaction. It may be inferred that absorption is localised in the caeca and that the trematode further digests the chyme of the eel.

The *excretory* vesicle is Y-shaped and lies towards the dorsal surface. Its pore is guarded by a muscular tube 0·047 mm. long, with a cuboidal epithelium. Beyond the sphincter as the vesicle passes between the testes, the wall becomes thinner. The vesicle branches just behind the ovary, and each limb continues forward near the side, till it reaches the level of the genital pore. Oblique sagittal sections show that the vesicle is made up of a thin membrane overlain by a widely spaced net of muscle fibres whose interstices are rectangular. The collecting tubes enter the terminus of each branch of the vesicle. A tangle of tubules is found around the entrance point, and it appears to have the form of a loop. The anterior duct branches some distance behind the pharynx and the ascending posterior duct branches near the vesicle. The branches from each end join as a loop, from one side of which arises the short tube to the vesicle; from the other side the tubule for a pair of flame cells.

For the observation of flame cells, the animals must be kept alive under the cover slip in isotonic saline. Stunkard's (1930) 0·4 per cent. Ringer solution is not so effective as a 0·8 per cent. solution containing carbonate.

According to the notation adopted from Looss (1894) by Cort (1919) and Faust (1922), the flame system of *Telogaster* is 2 (2 + 2) (2 + 2) or $2 \times 4 \times 2 = 16$. (Plate 14, fig. 3.) Each set of cilia is 0·016 mm. long, rising from an asymmetrical cell, with a large nucleus and nucleolus. The finer ducts are 0·002 mm.; the main ducts 0·004 mm. in diameter.

The *male genitalia* are simple. The morphologically right testis is smaller than the left in the ratio of 9 : 10. Usually the larger testis helps to produce the rather pointed form of the posterior end. Besides the germ cells, the testes have peripheral trophic cells similar to the shape of amphibian erythrocytes. (Plate 14, fig. 3.) Smaller not obviously cellular masses lie amongst them. These peripheral cells are vividly shown with $\frac{1}{1,200,000}$ neutral red and with Janus green in the metacerceria. They are strongly basophilic with haematoxylin.

The thin membrane surrounding each testis is continued anteriorly to form the muscular vas deferens. At about the level of the end of the caeca, the vasa fuse to run forward in the middle line dorsal to the uterus, which rests on the ventral body wall. The vasa lead into a short proximal lobe of the vesicula seminalis, which turns dorsally round the acetabulum to enter the distal seminal vesicle. A diffuse set of " prostate " glands lies in the parenchyma and connects with a thick-walled ejaculatory body. Near the genital

pouch the ejaculatorium fuses with the uterine metraterm to form a single thick-walled duct. There is a single muscular wall for the vesicles and the ejaculatory apparatus; so there is no cirrus pouch. No gonotyl was observed.

The *ovarian complex* lies between the forking of the excretory vesicle and the forking of the caeca. (Plate 14, fig 2.) There is a trefoil ovary of about half the volume of a testis. As variants there are spheroidal ovaries or ovaries almost completely separated into three lobes. Neutral red or Janus green causes trophic cells, half the diameter of those in the testes, to show clearly on the periphery of the ovary.

The ovary is in the middle line, and the oviduct arises from its dorsal face. This muscular tube enters the receptaculum seminis ventral to the exits of the other canals (Laurer and the uterus), all of which converge on the posterior end of the receptaculum. Laurer's canal leaves the receptaculum on the left hand side. At the level of the centre of the ovary it bends at right angles to open on the dorsal surface through a tight sphincter. It is a tube well provided with circular muscles, and in its lumen sperm have been observed in several specimens.

The uterus bends to the right from the receptaculum. First it receives the duct from the small yolk reserve. Then a fringing circlet of unicellular glands opens into it. Cilia line the posterior part of the receptaculum seminis, the anterior regions of the oviduct, Laurer canal and the uterus, all beating towards the receptaculum.

The vitellarium consists of strings of follicle groups developed dorsally and laterally between the anterior end of the testes and the posterior end of the caeca. Two main ducts, one from each side, fuse to make the small yolk reserve, which enters the uterus dorsally. The uterus makes one turn dorsal to the ovary, then crosses to the ventral surface, where it bends nine times—in young forms—before it reaches the acetabulum. Even when full of eggs it does not extend further back than the anterior end of the testes. A metraterm leads on to the genital pouch, after it has fused with the ejaculatory duct.

Uterine eggs are small (0·037 mm. long). Only a few follicles enter with each ovum, since the ovum occupies nearly all the space inside the shell. (Plate 15, fig 1.) Division occurs in the uterus, which becomes packed with several hundred eggs. An actively laying adult has the region from the anterior end of the testes to the acetabulum and from one side to the other filled with brown chitinoid eggs.

No miracidia have yet been hatched, but eggs have been incubated till they contained motile larvae. (Plate 15, fig. 2.) It appears that they must be eaten by *Potamopyrgus* before eclosion takes place.

Redia.

The larval stages of *Telogaster* are similar to those of *Cryptocotyle lingua* described by Stunkard (1930 b). Stunkard did not succeed in hatching eggs, nor did he find the sporocyst of *Cryptocotyle*, if such a stage exists; whilst *Cryptocotyle* has a redia and a lophocercous cercaria resembling those about to be described. Similarly no sporocyst of *Telogaster* has been seen, though it is difficult to

avoid the conclusion that the stage must exist in some form. And no generation of rediae by rediae has appeared at any time of the year.

Rediae develop in the adults of either *Potamopyrgus badia* Gould, 1848, *P. antipodum* Gray, 1843, or *P. corolla,* which are small fresh-water gastropods.

The dimensions are, for a mature redia of *Telogaster*, 0·95 x 0·20 mm.; pharynx 0·17 mm. diameter, gut 0·1 mm. long. They may be distinguished from the rediae of *Opechona** by the darker yellow of their gut contents. The birth pore has a flange-like opening just behind the gut. But it is readily visible only when cercariae are emerging. Germ cells are diffused, though they tend to aggregate in the posterior end, whence the cercariae develop. (Plate 15, fig. 4.)

Bedded in the cuticle are two sets of excretory tubes, one to each side. In each set, two flame cells lie in the parenchyma behind the pharynx, and two (sometimes three) lie about the middle of the length of the redia. Tubes from each flame cell join to form two main ducts, an anterior and a posterior on each side, which convolute greatly before they open by a single pore, one third of the total length from the anterior end. There are thus characteristically eight flame cells and two excretory pores in the redia. (Plate 15, fig. 3.)

Cercaria.

According to Lühe's system of 1909, the cercaria of *Telogaster* is a lophocercous monostome, or Sewell's (1922) pleurolophocercous cercaria.

The outline of its development in the redia is as follows. (Plate 15.) Germ masses 0·08 mm. long show a fine excretory tube on either side. No rudiment of the tail is differentiated, nor is there any other organ present. At a length of 0·18 mm. the narrow tail region forms and at its base the excretory tubes open, one to each side. (Plate 15, fig. 6.) The excretory tubes are still separate, but the loop at the top of the vesicle tube has appeared and the anterior and posterior collecting tubes rise from it close together. Differentiation of the oral sucker and pharynx has taken place.

When the body length is 0·20 mm. and the length of the tail 0 07 mm., the eye-spots have appeared as two pairs of faintly pigmented cells 0·008 mm. in diameter. (Plate 15, fig. 7.) The tail is constricted from the body. The excretory tubes from either side fuse posteriorly and grow wider to form the excretory vesicles. (Plate 15, fig. 8.) At the anterior end of the vesicles the tangle of collecting ducts forms.

Towards the end of development the tail fin, cuticular spines and penetration glands appear. (Plate 15, fig. 9.) The main excretory tubes become wider than the others, but the thick cellular lining does not arise until later.

Differentiation of organs takes place, then, in this order: Excretory tubes, oral sucker, pharynx, body muscles, eye-spots, tail, excretory vesicles, penetration glands, cuticular spines and finally the tail fin.

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* *Opechona stegadexamene* is a trematode parasitising eels, with the same larval stage hosts as *Telogaster*.

When naturally emerged from the mollusc the cercariae are pyriform and are 0·24–0·30 mm. long by 0·11 mm. wide at the widest part when not extended. The oral sucker has a diameter of 0·045 mm.; and the tail is 0·34 mm. long by 0·042 mm. wide, with a fin 0·04 mm. high. (Plate 16, fig. 2.)

In the anterior region the cuticle is beset with rows of spinules which are longest in front of the mouth, but become progressively smaller backwards till at and beyond the level of the eye-spots they are buried in the cuticle. Posteriorly only minute rudiments of them are present. The penetrating snout lies dorsal to the mouth, where the loose lips may close forward and ensheath the snout. On the snout process there is a group of modified spines set perpendicularly to the surface. Each spine is 0·007 mm. long (twice the length of the cuticular spines), and the set has a nearly constant arrangement, though the numbers of spines vary from 14 to 16. (Plate 16, fig. 4.)

The excretory pores open on the tail on each side near the anterior end. Proximally the cuticle of the tail is loose for a short distance. At the point where the cuticle tightens the fin arises from the mid-dorsal surface to continue round the end of the tail with very little decrease in height. (Plate 16, fig. 1.) On the ventral surface the fin proceeds forward only about a quarter the length of the tail. Beneath the cuticle there are circular and longitudinal muscles over a matrix of reticulating cells and formative cells.

It has already been seen that the mouth is nearly terminal and that it is surrounded by spine-bearing lips. The oral sucker is large, acting as a drum over which the cuticle may be stretched. In the cercaria a prepharynx, pharynx and a short length of oesophagus are formed. There are no caeca.

Dorsal to the pharynx, and just behind it are the ganglion lobes. Sections show the main nerve tracts on one side to be a pair to the oral sucker, a ventral which later becomes lateral, a lateral which remains lateral and a dorsal which does not seem to continue further than the excretory vesicles. The eye-spots are rectangular in shape, being made up it seems of two cells each. If this is so, the pigment spherules have collected on the periphery of the cells where they touch each other. as though on the narrow waist of an hour glass, There is a small cup at either end free of pigment.

As Stunkard (1930 a) maintains, a $\frac{1}{1,000,000}$ solution of neutral red is the best means of showing up the penetration glands. Intra vitam the cytoplasmic granules stain neon red, but the nucleus remains clear. Secretion in the ducts or outside the animal also stains, so that the reaction—if the work on azine and azonium dyes summarised by Koehring (1930) be correct—suggests the histolytic nature of the secretion. There are 25 gland cells (range of counts 23–26). The ducts are collected into two main sets on each side, which separate widely as they swing dorsally round the oral sucker to open in an arc round the dorsal edge of the penetration snout. Exact counting of the number of ducts is difficult but they are typically arranged at their openings in four sets of six, with three in each tier of a set.

The excretory system is nearly the same as that of the adult. The vesicle is Y-shaped, but its wall is made up of large irregular cells with finely granular and opaque cytoplasm. The granular inclusions suggest a secretory function. From sections it is seen that four to six cells surround the relatively minute lumen. The loop arrangement of the collecting tubes is the same as in the adult. There are sixteen flame cells 0·007 mm. long, distributed 2 (4 x 2).

Sections stained with iron haematoxylin show that masses of formative cells lie to the outside of the excretory vesicles. Between the arms of the vesicles there are two groups of cells (dorsal and ventral) smaller than formative cells and staining almost completely black. Stunkard (1930 b) doubts whether they are genital anlagen in *Cryptocotyle,* and suggests that they are ready to form the acetabulum. Certainly they are in the wrong position for testes in *Telogaster,* but not for the ovary. Their staining indicates that some of them may migrate laterally to form the gonads. The staining of the gonads of metamorphic specimens is similar, but not identical so that renewed inquiry is needed.

Metacercaria.

Metacercariae have been found in the muscle of *Gobiomorphus* spp., *Philypnodon* spp., *Galaxias brevipennis, Galaxias attenuatus,* and young brown trout, *Salmo fario,* these being the chief small fish of Canterbury rivers. The *Eleotrids* and *Galaxias brevipennis* are the most heavily infected; *Galaxias attenuatus* and the trout carry only a few cysts.

Penetration by the cercaria of *Telogaster opisthorchis* has been observed by making hanging drop preparations of freshly removed fins or muscles of bullies in Ringer solution. The cercariae were kept in $\frac{1}{1,000,000}$ neutral red in Ringer solution till the penetration glands became bright red. In this condition the cercariae were vigorous. When placed on the fish muscle they drew themselves over the mucous film, then suddenly attached themselves by the oral sucker. The tail was shaken off by five or six convulsive twists of the posterior end of the cercaria. While the cercaria adhered vertically to the flesh, the flanks twitched, probably to drive enzymatic material forward. At the end of a minute sufficient dissolution had taken place for the cercaria to force itself in. This process is possible as mentioned above, because of the drumlike form of the oral sucker. The penetration snout and its spines are thrust forward by the oral sucker so that the lips and lateral spinous cuticle are drawn back. (Plate 16, figs. 3a, 3b.) As they go back they tend to grip the tissue being penetrated, and thus pull the cercaria further in. The mouth then anchors the head end, and the lips are again drawn forward in front of the penetration snout. In doing so the spines of the cuticle are thrust out by the oral sucker. They grip the host tissue and as the oral sucker moves forward again, exert an abrasive effect. Penetration is due partly to the action of the enzymes, partly, it appears to the tearing action of the cuticular spines. The penetration spines are of use possibly in piercing the tissue ready for the enzymes to enter, but they have no raking effect such as the cuticular

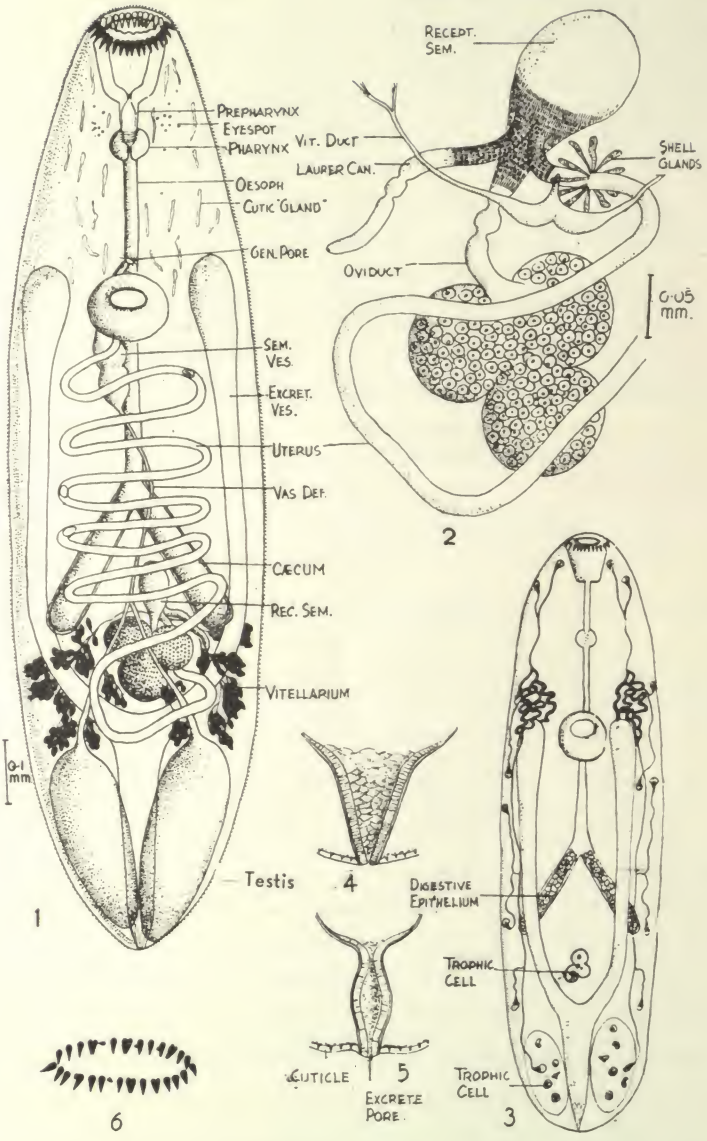

FIG. 1.—Adult *Telogaster opisthorchis*, ventral aspect.
FIG. 2.—Ovarian complex from the dorsal side.
FIG. 3.—Excretory system.
FIG. 4.—Sphincter of excretory vesicle open.
FIG. 5.—Sphincter closed.
FIG. 6.—Teratological variation of the cephalic spines.

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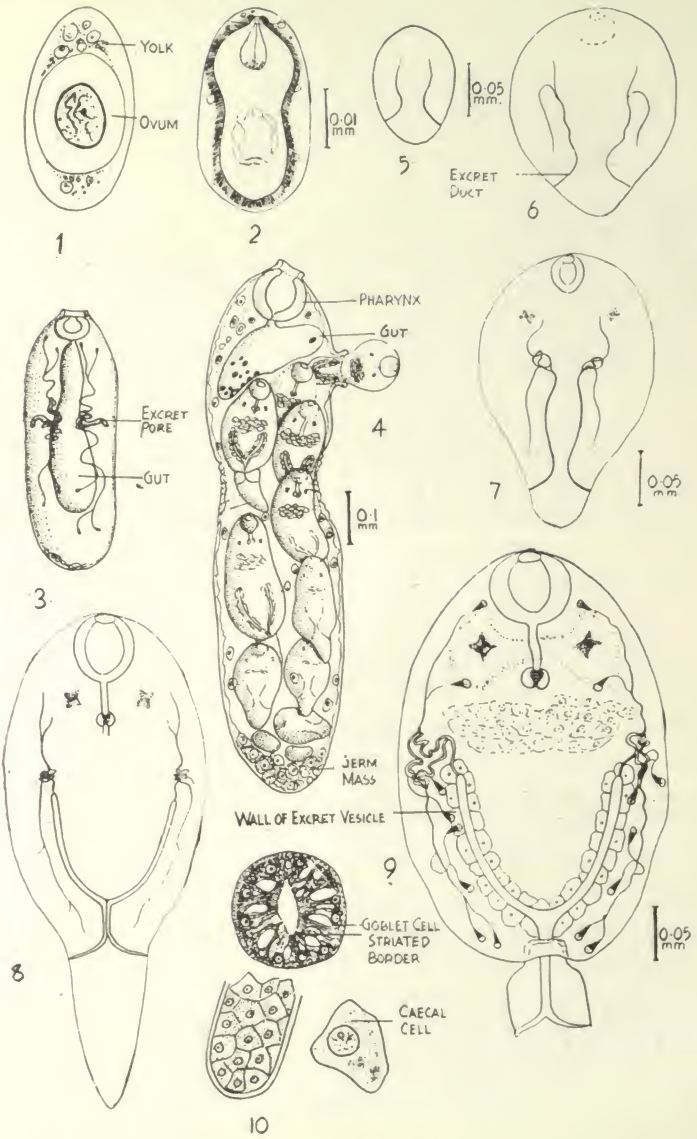

FIG. 1.—Egg, newly formed, in the uterus of *Telogaster*.

FIG. 2.—Miracidium in egg.

FIG. 3.—Young redia of *Telogaster*.

FIG. 4.—Mature redia.

FIG. 5.—Early stage of cercaria of *Telogaster* in the redia. The first two excretory tubes are developed.

FIG. 6.—The excretory tubes are branched.

FIG. 7.—Eye-spots, tail rudiment and oral sucker have appeared in the cercaria.

FIG. 8.—The excretory tubes have fused at the base of the tail and the collecting tube loop is formed.

FIG. 9.—Mature cercaria showing the excretory system complete and penetration glands and snout formed.

FIG. 10.—T. S. of caecum to show the digestive epithelium.

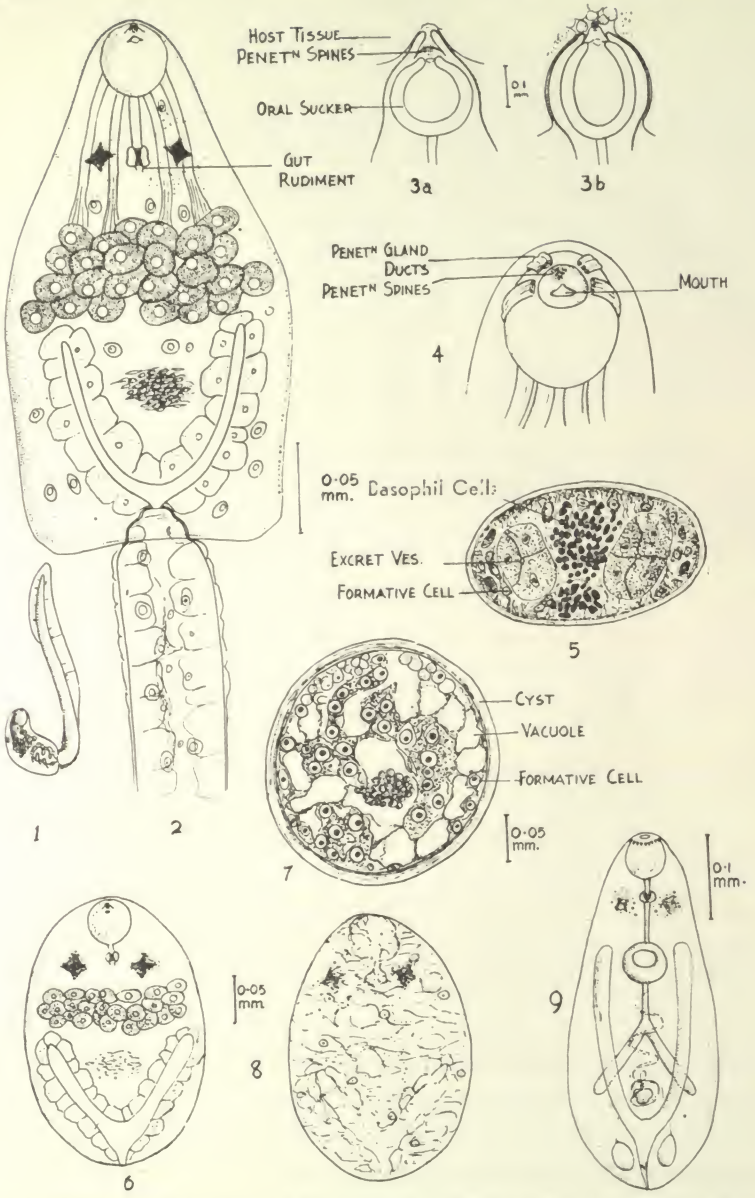

FIG. 1.—Swimming attitude of the cercaria, showing the form of the fin.
FIG. 2.—Cercaria of *Telogaster*, ventral aspect.
FIG. 3A.—Ventral view of anterior end of cercaria beginning penetration. The oral sucker is circular, the lips are thrust forward and the penetration snout is drawn in.
FIG. 3B.—Ventral view of cercaria with the lips drawn back, the penetration snout thrust forward and the oral sucker elongated. Enzyme is exuded during this movement.
FIG. 4.—Ventral view of oral sucker and penetration apparatus.
FIG. 5.—T. S. through excretory vesicles and possible gonads.
FIG. 6.—Cercaria of *Telogaster* newly penetrated into the host tissue.
FIG. 7.—T. S. cyst of *Telogaster*. There is practcally no secondary cyst.
FIG. 8.—Metamorphosis of the metacercaria.
FIG. 9.—Young metacercaria with recently formed testes, acetabulum, gut and cephalic spines.

spines have. Their only movement is backwards and forwards parallel with the direction of motion—like a plunger.

These cercariae did not encyst in the fin membrane—they wandered up and down between the two epidermes till they died. This is in accordance with the observation that metacercariae of this species never occur on the fin, though specimens of *Opechona* are not uncommon in that position. Cercariae penetrate the fins and encyst in the pectoral muscles or make their entrance through the snout, eyes or dorsal fin. They do not appear to be able to produce lysis of the scales of the fish. This accounts for the high concentration of cysts in the mid-dorsal line and pectoral muscles. Encystment takes place mostly in the muscles. It takes three minutes for the cercariae to enter the tissue completely: in about half an hour they have found a suitable place to encyst and they begin to revolve slowly. After four hours no cyst wall can be seen, but the red cercariae still revolve about a fixed point. At twelve hours from the initial penetration the cercariae still move round and round, but a delicate hyaline cyst-wall has been formed. Stunkard suggests that the penetration glands also secrete the cyst wall; certainly there are no other obvious glands to do it. Yet the penetration glands are not reduced visibly from the size of those in the free cercaria after the cyst has been formed. There is no observation that would account for the formation of the primary cyst.

One cercaria, under a cover glass, burrowed through an immature cercaria of the same species that it encountered. The cuticle of the full grown cercaria must be impervious to the enzyme, so that either the younger cercaria is not resistant or else friction and abrasion are necessary concomitants of penetration.

The stages of development of the metacercaria are the encysted cercaria, the stage of de-differentiation, the growing adult-form and the progenetic metacercaria.

(a) The newly encysted animal is essentially a cercaria. Its penetration glands disappear, but its penetration spines and the thick wall of the excretory vesicle are retained. (Plate 16, fig. 6.)

(b) Metamorphosis takes place shortly after the disappearance of the penetration glands at a cyst diameter of 0·25 mm. A secondary fibrous cyst is provided by the host, but this membrane is usually no more than a semi-opaque film round the transparently smooth primary cyst. In a single bully the contrast between the *Opochona* and the *Telogaster* cysts is marked by the cellular, thick secondary cyst of the former and the almost invisible secondary of *Telogaster*. (Plate 16, fig 4.) The differential response of the fish to the two parasites has no obvious explanation; but a set of injection and grafting experiments might help to elucidate it.

Metamorphosis involves the practically complete dissolution of all formed organs of the cercaria and their reconstruction. New organs develop also. (Plate 16, fig. 8.) The penetration spines and penetration glands are lost rapidly. The

cytoplasm of the parenchyma and oral sucker develop large vacuoles and refractive globules appear. From sections it is seen that the nuclei and nucleoli of the formative cells are intact, but the large cells of the excretory vesicle have disappeared. Formative cells aggregate to form the intestine and the acetabulum, and the gonads are defined as masses of compact cells stained darkly with haematoxylin. This process is very similar to de-differentiation and regeneration in Triclads (Curtis, 1933), and a stimulatory mechanism for it might be found in terms of the new environment of the cercaria in the muscle.

(c) The re-formed metacercaria, although its parenchyma remains irregular for some time, is equipped with the essential organs of the adult. (Plate 16, fig. 9.) Cuticular spines 0·004 mm. long again become visible, and an anterior row of such spines is modified to form cephalic spines. The smallest cephalic spines seen have been 0.006 mm. long, concave ventrally and of the same wedge shape as the ordinary body spines. There can be no doubt that they are modified cuticular spines. The shape, staining (densely basophil) and position in a region where no cuticular spines are present all confirm the homology. This tends to make tenable the opinion of van Cleave (1922) and Yamaguti (1934) that, although *Caecincola* and *Cryptogonimus* are without cephalic spines, they should be included in the same subfamily (Cryptogoniminae) as *Allacanthochasmus* and *Paracryptogonimus,* which possess spines. Since differential growth is the cause of the presence of the long spines their view may be justifiable.

Cephalic spines 0·007 mm. long appear when the metacercaria is 0·45 mm. long, though there is some variation in the length of the animal. By the time the trematode has reached a length of 1·20 mm. the spines are full-grown at 0·050–0:052 mm. If the body length increases after this stage, the spines do not grow further. Thus the spines (when the body is 1·2 mm. long) have increased nine times in length while the linear increase of the body has been three. In the same period the larger testis quadruples its length from 0·06 mm. to 0·25 mm., or the ratio of its length to that of the body changes from about one-seventh to one-fifth. Accordingly, it is growing faster than the body, but not so fast as the cephalic spines.

Figure I shows these relationships. The relationship between the testis and body lengths is linear and may be expressed as $y = bx$. (y = length of testis, b = a constant 0·157, x = length of body.) So that $y = 0{\cdot}157x$.

But the curve relating spine length to body length is markedly different. It does not pass through zero, so that a certain threshold of body length must be obtained before any growth of the spine takes place. The initial steep growth flattens out till at a body length of 1·2 mm., little further growth of spines takes place. This curve resembles the parabolic curve of heterochronic growth. (Shaw, 1928, and Tazelaar, 1930.) The general growth corresponds closely with that of the horns of titanotheres, in which a certain body size was necessary before the horn appeared.

The experimental curve, with the data smoothed by a sliding mean of three method, fits closely to the curve of the equation

$$y = \frac{x - d}{bx - a} + c.$$

where y = length of cephalic spine in mm.
x = length of body in mm.
a = constant.
b = constant.
d = threshold of body length at which spines appear.
c = length of body spines, from which cephalic spines develop.

so $$y = \frac{x - 0{\cdot}45}{17{\cdot}6x - 1{\cdot}5} + 0{\cdot}0075.$$

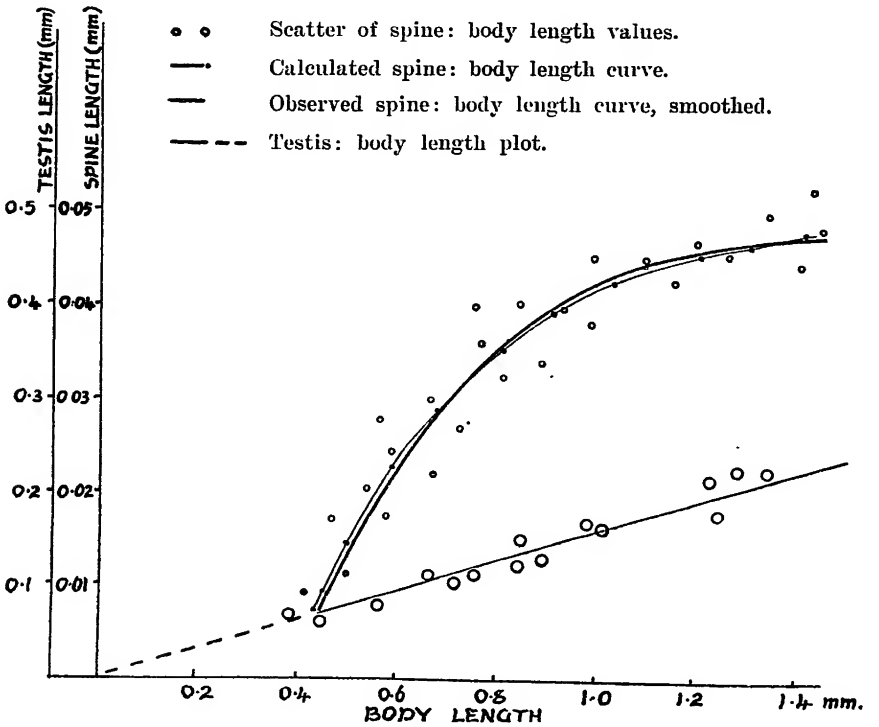

FIG. 1.—Curves showing the relation between body length and testis length during growth of the metacercariae; and the heterochronic growth of cephalic spines relative to body length.

The spines begin to develop usually a little earlier than the time the testes are defined, and there is no indication from the growth curves of a direct interaction between the two organs. The testes grow slightly faster than the body, the spines much faster. Possibly they both respond to the same stimulus. Usually it has been held, however, that the gonad of invertebrates does not influence the development of other characters.

In the post-metamorphic cercaria the scattering of the eye-pigment is not so marked as it is in *Opechona,* and it does not take place to the same extent in each eye-spot.

Formative cells are moulded into the caecal tubes.

At this stage the excretory vesicle becomes filled with spherules of excreted material, the maximum diameter being 0·012 mm. This is twice the size of those of *Opechona,* so that the two cysts are readily distinguished in the host by the bifid darker vesicle of *Telogaster* and the single white vesicle of *Opechona,* which reflects more light. The excreta are stored and released after excystment in the final host.

A system of granular cells resembling in form the prostate, shell and penetration glands, becomes evident in metacercariae about 0·85 mm. long. The cells are spread dorsally from the cephalic spines across the region of the ganglia, and a narrow band continues backwards to the ends of the caeca. The cytoplasm of the cells is filled with coarse granules in Brownian movement, this material continuing into the ductules which interramify amongst the cells. These cells are rarely seen in the adult. The long oxyphil cuticular structures of the adult do not appear till the metacercaria is 0·9 mm. in length.

(d) Progenetic *Telogaster* metacercariae are uncommon and easily overlooked because of the transparency of the egg shells. The cyst is large, 0·60 mm. in diameter. All the adult characters have appeared though the excretory vesicle is filled with metacercarial granular excreta. Malformed eggs are commonly present in the uterus of younger specimens, but mature metacercariae produce up to twenty viable eggs, which lie free in the cyst. Motile miracidia have been grown with the eggshells, but none has hatched. Hatching probably takes place in the intestine of *Potamopyrgus,* though this has not been confirmed for *Telogaster.*

Taxonomy.

Telogaster is similar to *Paracryptogonimus acanthostomus* Yamaguti and *Allacanthochasmus varius* van Cleave. It differs, however, in having the caecal bifurcation posterior to the acetabulum and in the terminal location of the testes.

Poche (1926) and Yamaguti (1934) would have placed these genera in the family Acanthostomidae Poche (1926). Meuller and van Cleave (1932 and 1934) consider, on the other hand, that Allacanthochasmus should be included in their Neochasminae (Heterophyidae) on account of the structure of its genital pore. Others of Poche's Acanthostomes without a gonatyl—*Cryptogononimus* and *Caecincola* —they include in the Heterophyidae.

In 1939 Faust suggested that there should be a superfamily Heterophyoidea to include the families Heterophyidae Odhner, 1914, Michrophallidae Viana, 1924, Cryptogonimidae Ciurea, 1933 and ? Lecithodendriidae Odhner, 1910. But Mueller and van Cleave (1932) had reduced the Cryptogoniminae Osborn (1910) and Ward (1917) to part of the Heterophyinae Ciurea (1924). Since there is, however, considerable unity of structure amongst the Cryptogonimidae it is proposed here to follow Faust in retaining them as a family in the superfamily Heterophyoidea. Witenburg (1929) redefined the family

Heterophyidae, and this was extended by Mueller and van Cleave (1932). This in turn became the essence of Faust's Heterophyoidea (1929 emended 1939).

Ciurea's Cryptogonimidae (cf. Ward, 1917) are small spinous trematodes with or without oral spines. Prepharynx and pharynx present, Y-shaped excretory vesicle, flame cells 2 (1 + 1) (1 + 1), testes of the posterior third, no cirrus or cirrus pouch, ovaries lobed, eggs small. *Telogaster* shows close affinity with this subfamily. Of the Heterophyoidea only some genera have circumoral spines. These are *Allacanthochasmus* van Cleave, 1922, *Neochasmus* van Cleave and Mueller, 1932, and *Paracryptogonimus* Yamaguti, 1934. From all of these *Telogaster* differs in having posterior parallel testes and bifurcation of the digestive tract posteriorly to the acetabulum. The larval forms and the general adult structure place the genus near the Cryptogonimidae.

Generic diagnosis: 22–34 cephalic spines in adult, eye-spots present, testes at extreme end, vitellaria between anterior end of testes and posterior end of caeca. Uterus not extending to the posterior end. Prepharynx long, oesophagus very long, bifurcating posterior to the acetabulum. Flame cells 2 (2 + 2) (2 + 2). Cercaria lophocercous with 23–26 penetration glands.

SUMMARY.

1. The anatomy of a Cryptogonimid (Heterophyoidea) trematode occurring in the ileal sector of the intestine of New Zealand freshwater eels is described.

2. The miracidium, redia, cercaria, metamorphic cercaria and metacercaria have been studied.

3. The life cycle passes from the adult in *Anguilla* spp. to the redia in the freshwater gastropods *Potamopyrgus* spp. thence to the metacercaria in the small freshwater fish *Gobiomorphus* spp., *Galaxias* spp., and *Philypnodon* spp.

4. This parasite is considered to be a new genus and new species, *Telogaster opisthorchis,* and its taxonomy is discussed.

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